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# Systematics of the Genus *Monolena* (Melastomataceae) in Central America

by

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Morphological, anatomical, and field studies indicate that *Monolena* (Melastomataceae) is represented by eight species in Central America. Seven of these species are found in Panama: *Monolena grandiloba*, *M. dressleri*, *M. multiflora*, *M. panamensis*, *M. morleyi*, and *M. trichopoda*, newly described and all endemic to Panama, and *M. priumliflora*, which ranges from eastern Costa Rica to southern Peru. The eighth species, *M. guatemalensis*, is endemic to Guatemala. Taxonomic accounts of these species are presented, along with notes on anatomy, cytology and distribution.

The genus *Monolena* (Melastomataceae) consists of 14–16 species with an overall distributional range from Guatemala to southern Peru and Acre, Brazil. The group is distinguished from other members of the Melastomataceae by the combination of: (1) its herbaceous habit, in which the stem is reduced to a fleshy rhizome; (2) its 1-sided pedunculate and bracteate cyme (or 1-flowered scape); (3) its 3-1ocular ovary in an otherwise 5-merous flower; (4) its dimorphic androecium; (5) its anthers, each of which has the connective ventrally extended between the thecae and the insertion of the filament and further extended to form a large or small ventral appendage; and (6) its triquetrous capsular fruit. Members of the genus are mostly epiphytic, growing on lower trunks and branches, buttresses, stumps, logs and rocks, or sometimes on the ground.

### TAXONOMIC HISTORY

The earliest description of *Monolena* was provided by J. J. Triana *in* Bentham and Hooker (1867). Triana had collected several species of *Monolena* from western Colombia and had apparently seen other collections from Peru, but he described no species and cited no specimens with the first generic description. *Monolena primuliflora* Hook.f. was the first species described, that being done in 1870.

A later publication from Triana (1871) described one species from western Colombia. Cogniaux (1891) and Gleason (1930) each published a species from eastern Colombia, and Uribe (1960, 1971, 1979) described four more species from western Colombia. Prior to the present paper, *Monolena guatemalensis* Donn. Sm. was the only species of *Monolena* described from Central American plants. *Monolena* was treated in regional floras for Guatemala (Standley and Williams 1963), Panama (Gleason 1958), Ecuador (Wurdack 1980), and Peru (MacBride 1941). The genus belongs to the New World tribe Bertolonieae; that tribe could possibly be merged with the Old World Sonerileae (Wurdack 1980). A revision of *Monolena* became necessary when many diverse new taxa were discovered in Panama.

### MATERIALS AND METHODS

Investigative approaches by the author included a review of herbarium material; field research in Costa Rica, Panama, Colombia, and Ecuador; anatomical and cytological studies; and observations made from plants cultivated in greenhouses at the University of Minnesota. Cytological material was studied from immature flowers fixed in the field with Carnoy's solution (4:3:1 absolute alcohol, chloroform, glacial acetic acid) and kept as close to 0°C as possible for 1–3 days, after which the material was stored refrigerated in 70% alcohol. Anthers were teased open, squashed with acetocarmine solution and permanently mounted in Hoyer's fluid.

### DISTRIBUTION AND HABITAT

The greatest diversity of *Monolena* species is found in Panama and western Colombia. Five or six species are found only in the Serranía de Baudó, Río Atrato basin, Pacific lowlands, and the west flank of the Andes in Colombia in the departments of Chocó, Valle, Cauca and Nariño (Uribe 1971). Another six species are endemic to Panama and newly described here: *Monolena dressleri*, *M. grandiloba*, *M. morleyi*, *M. multiflora*, *M. panamensis*, and *M. trichopoda*. In Panama, *Monolena* occurs along the crest of the cordillera in the vicinity of the continental divide, the Caribbean slope of the cordillera, and occasionally in the Caribbean lowlands. (Fig. 1)

Monolena primuliflora is the only widespread species of Monolena, occurring from southern Costa Rica to southern Peru. Monolena guatemalensis is known only from Guatemala, nearly 900 km from its nearest congener.

Monolena are primarily herbs of wet tropical forests and cloud forests. In Panama they typically occur in regions of tropical premontane rain forest and tropical wet rain forest (Tosi 1970). In these regions the dry season, from about December through April, is often interrupted by periods of rain; fog and mist are common throughout the year.

Monolena most often grows as epiphytes on tree trunks, buttresses and branches within three meters of the ground. One collection of *M. guatemalensis* was reported as growing near the top of a tree. Most or perhaps all species of Monolena also grow on decaying stumps and logs or occasionally as terrestrials. Monolena dressleri and M. trichopoda, and some populations of M. grandiloba, M. multiflora and M. primuliflora, typically grow on rocks in streams.

### COMPARATIVE MORPHOLOGY

GROWTH HABIT. — Plants of *Monolena* are herbaceous; the vegetative shoot axis is condensed into a fleshy, green to brown rhizome. The rhizomatous habit, anomalous in the Melastomataceae, creates some difficulty in determining phyllotaxy in the genus. The leaves are basal and are borne in clusters on the rhizome; each cluster appears to represent a developed bud, with no elongation of its axis. The first visible structures of the expanding bud are 4–6 small scales that are opposite and decussate, as would be expected of a Melastomataceae. The foliage leaves then appear, but they are borne singly, not in pairs, and hence Triana (1871) wrote that they appeared to be alternate. However, with the leaves appear a few more scales, and sometimes one of these is found approximately opposite each new leaf, although the opposite position of a given pair changes as the rhizome and leaf base enlarge. Triana proposed that such a paired scale represented a vestigial member of a pair of opposite leaves.

ROOTS. — *Monolena* roots are generally fibrous and are usually entwined in a substrate of vegetation and partially decomposed litter. The larger roots are few in number, white, glabrous, and round in cross-section. The rootlets are more abundant, brown, round to square in cross-section, with a cylindrical core and an easily removed outer sheath. The rootlets are glabrous to pubescent. The hairs are

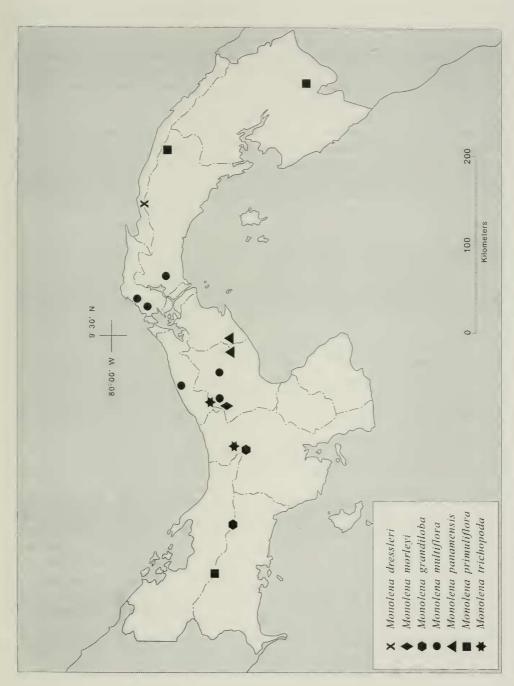


FIGURE 1. Distribution of Monolena in Panama.

usually stiff and retrorse and apparently aid in anchoring the plant to the substrate. Rootlets are often attached to partially decomposed substrate, perhaps affixed by mycorrhizae.

LEAVES. — The leaves of *Monolena* are well differentiated into petiole and blade. The petioles are canaliculate and vary from slender in the small, delicate species, to thick and succulent in the more robust species. The upper blade surface is shiny green, although occasionally the primary veins are red-purple. In *M. dressleri* and its South American allies, the upper blade surface is usually very dark green with a metallic luster (this group of species includes *M. bracteata* Gleason, *M. cordifolia* Triana, *M. dressleri*, *M. pilosiuscula* L. Uribe, and *M. pygmeae* L. Uribe; it is hereafter referred to as the *Cordifolia* complex). In most species the lower blade surface and petiole are red-purple, although sometimes they are so colored only along the veins, other times in the areoles, and occasionally not at all. The texture varies from membranous to subcoriaceous. Blade morphology is variable, but generally consistent within a species. Blades vary from elliptic to lanceolate, ovate, or round. The margins vary from rarely entire (only in *Monolena trichopoda*), to more often ciliolate-serrulate and occasionally repand, to crenate-dentate and ciliolate in the *Cordifolia* complex.

As in most Melastomataceae, foliar venation in *Monolena* consists of 3–11 longitudinal nerves, called primaries. Including the midrib, the number of primaries is always odd. The outermost pair of primaries is usually inconspicuous and converges with the margin in the lower 2/3 of the blade. Leaves in *Monolena* vary from nerved to strongly plinerved. Leaves are referred to as "nerved" when all of the primaries arise from a common point at the base of the blade (see Fig. 2B), or "plinerved" when one or more pairs arise from the midrib above the base of the blade (see Fig. 3B; Almeda 1978). Leaves of *Monolena* species are, with very few exceptions, consistently nerved or plinerved, an easily observed character useful to distinguish species. The secondary veins sometimes run between and connect the primaries, or with the tertiary veins form a reticulate pattern. The primary veins, and occasionally the secondary veins, are raised below and sometimes depressed above the leaf surface.

In all but one species of *Monolena* in Central America the petiole and lower blade surfaces are minutely puberulent, while the upper surfaces appear glabrous but actually bear scattered minute hairs. *Monolena morleyi* is distinct in the genus for being glabrous. *Monolena trichopoda* exhibits a distinct, but often caducous fringe of hairs along the ridges of the petiolar canal, and is the only Central American species having large trichomes on the upper blade surface, in addition to the smaller hairs mentioned above. However, the large trichomes on the blades of *M. trichopoda* are rare, apparently found only on juvenile leaves, and may be present only on some leaves of a given plant. The South American species display a greater diversity of trichome types, including some that are peculiar to certain species, as in *Monolena pilosiuscula*, which has sclereids present in the base and shaft of the foliar trichomes.

Sclereids of a different type are found in the leaf blades of some species of *Monolena*. *Monolena* panamensis, M. morleyi, M. grandiloba, M. primuliflora, and some South American species have sclereids in the hypodermis of the upper surface of the blade. The shape and the abundance of sclereids in M. primuliflora vary considerably, and they are mostly lacking from plants of lower elevations in Chocó, Colombia, southeastern Peru, and probably in plants of lower elevations in the Talamanca Mountains of Costa Rica and Panama. Leaves of M. multiflora have sclereids in the hypodermis of both the upper and lower blade surface and, as in M. primuliflora, the density of sclereids is sharply reduced in plants from lower elevations, specifically those populations from Río Guanche, Colón province, Panama. Most plants of M. trichopoda lack foliar sclereids, but where they do occur, they are found only in the hypodermis of the lower blade surface. Foliar sclereids are completely lacking in M. guatemalensis and members of the Cordifolia complex.

INFLORESCENCE. — The inflorescence in *Monolena* is a scorpioid cyme (Triana in Bentham and Hooker 1867; Cogniaux 1891). More specifically, it is a circinnately coiled cyme, with the flowers alternating from one side to the other, along one side of the pseudoaxis. This type of inflorescence is apparently derived from a dichasium by suppression of successive axes on alternate sides. The peduncle

varies from green to red and from fleshy to very succulent. The number of flowers per inflorescence ranges from 3 to 35 in the Central American species. Members of the *Cordifolia* complex in Chocó, Colombia mostly have 1 or 2 flowers per inflorescence.

Associated with the inflorescence are three types of bracts that can be distinguished by their position relative to the flowers: (1) scales, which are borne on the peduncle below the lowermost flower and its floral bracts; (2) lower floral bracts, which subtend each flower; and (3) lateral floral bracts, which are borne to the outside of the two rows of flowers. The latter two types of bracts are indistinguishable from one another, except by position, and are here collectively referred to as floral bracts.

The scales are somewhat foliaceous, usually green and with venation similar to that of the leaves. The floral bracts are petaloid, although more succulent than the petals, translucent green to white, and have parallel venation like that of the petals. The floral bracts are obovate, except in *M. multiflora*, where they are broadly ovate to round or reniform. The floral bracts envelop the flower buds until shortly before the flowers open. In *M. multiflora*, the floral bracts form a tightly closed sac around the flower buds.

One lower floral bract subtends each flower, a character consistent throughout the genus. Most species also bear one lateral floral bract per flower, and four scales per inflorescence. Variation in the number of scales per inflorescence is seen in the wide-ranging *M. primuliflora*, which has two or four (rarely six), and in *M. trichopoda* which has two or (in some cases) apparently only one. In *M. panamensis, M. multiflora*, and *M. grandiloba* the lateral floral bracts are approximately half the number of the flowers. These species also bear the greatest number of flowers found in the genus. In *M. guatemalensis*, only the two lowermost lateral floral bracts are apparent on the available material.

The floral bracts appear to represent pairs of opposite bracts that have been displaced by the shifting of the flowers to one side of the pseudoaxis and by the swelling and elongation of the pseudoaxis. Although not readily observable in the floral bracts, such a shift in relative position is evident in the scales on the peduncle. Initially, the scales are approximately opposite and decussate, but are displaced vertically as the inflorescence elongates.

FLOWERS. — **Hypanthium and Perianth**. The *Monolena* hypanthium is obconical to turbinate and slightly constricted where it surpasses the apex of the ovary; in cross-section, it ranges from round to triangular. It is 10-nerved and crowned by a highly vascularized region, the torus, which is the point of insertion of the perianth and stamens.

The calyx lobes are usually connate at the base to form a short tube. The lobes are triangular and rounded at the apex in most species. The calyx lobes in *M. multiflora* are rounded at the apex or more often emarginate, and in *M. grandiloba* the lobes are exceptionally large, broader at the apex and deeply obcordate. In some South American species, the calyx lobes are spathulate. The margins of the calyx lobes are ciliate in all species of *Monolena* and, in most species, the hypanthium and calyx are sparsely puberulent. Notable exceptions are *M. panamensis* and *M. morleyi*, in which the hypanthium and calyx lobes are glabrous.

The petals in *Monolena* flowers are five, convolute in the bud, and free. In most species, the petals are broadly obovate to oblong and spread to form a shallow cup upon opening. The corolla varies from pink to white within some species, either as solid colors or white at the base and pink toward the apex. In other species, it is strictly pink or white. In some plants of *M. multiflora*, the petals are pink-striped with translucent white veins. *Monolena grandiloba* has been described by collectors as having petals "clear pink" or "bright pink."

Androecium. The ten stamens in *Monolena* flowers are disposed in two whorls of 5. The two whorls are morphologically distinct in that the antesepalous stamens bear a more complex and diverse connective and are mostly 20–40% larger than the antepetalous stamens. The filaments are white, dorsiventrally compressed and are declined to one side when the flower opens. The thecae are yellow, linear, and tipped by a ventrally inclined terminal pore. In bud the stamens are strongly inflexed; the apex of the thecae rest between the hypanthium and the ovary.

As in most Melastomataceae, the connective in *Monolena* is a complex structure, useful in distinguishing both the genus and the species. The connective is geniculate just below the thecae, so that the lower portion of the connective, and the ventral appendage in particular, is positioned between the thecae and the style. The ventral appendage is the enlarged basal portion of the connective. The dorsal side of the connective is grooved from below the geniculation to the insertion of the filament. The groove often continues along the ventral appendage, although it soon becomes indistinct. On the antesepalous stamens, and occasionally on the antepetalous ones, the upper end of the groove terminates in a small tubercle. The groove embraces the filament when in bud. In the antesepalous stamens the ventral appendage varies from subglobose in most species to tongue-shaped in *M. trichopoda*, saddle-shaped in *M. dressleri*, and geniculate and pointed in *M. grandiloba*. The antepetalous stamens bear only a small linear ventral appendage, or occasionally none at all. In most species of *Monolena* the entire connective is yellow. Exceptions are found in *M. grandiloba* and some populations of *M. multiflora*, in which the ventral appendage and dorsal surface on the antesepalous staminal connectives are pink (but turn black on drying).

**Gynoecium**. The ovary in *Monolena* is 1/2–3/4 inferior, 3-angled in cross-section, and trilocular. The apex of the ovary is excavate, with the style emerging from the center. The style is narrow at the base, swollen near the middle, and slightly contracted and curved below the capitate, papillose stigma. The numerous ovules are born on axile placentas that are narrowly deltoid in section and intrude into the locules. The ontogeny and anatomy of the similar gynoecium in *Bertolonia marmorata* were described by Van Heel (1958).

**Fruit and seeds**. The *Monolena* fruit is a triquetrous capsule; dehiscing by valves that open at the top of each locule. The hypanthium is shed as the ovary matures. The seeds are obconic-pyramidate, with a lateral raphe along most of their length. The surface patterning varies from inconspicuously roughened to papillate. Seed morphology of *Monolena* was further described by Whiffin and Tomb (1972).

### FLORAL SYMMETRY AND POLLINATION

Symmetry in flowers of *Monolena* is radial with respect to the perianth, but bilateral with respect to the androecium and gynoecium. The open flowers face at an angle of 0–90 degrees above horizontal. The stamens are declined to the lower side. The style is bent just below the apex so that the stigmatic surface and thecal pores face toward each other.

As in many taxa with poricidal anther dehiscence, *Monolena* flowers are probably pollinated by buzzing insects. In buzz pollination, vibrations created by the insect cause pollen discharge. Although I observed six species in bloom in the field, few potential pollinators were seen visiting *Monolena*. Insects believed to be bees were observed leaving flowers of *Monolena panamensis*, and were seen to inspect, but not land on, flowers of *M. pilosiuscula*. The insects were presumably foraging for pollen; no nectar or oil is produced in *Monolena* flowers, which are also odorless.

An apparent mechanism for self-pollination is present in plants of the *Cordifolia* complex, in *M. trichopoda*, and possibly in other species as well. Late in anthesis the connective folds in such a way as to cross the thecae over, or to the side of, the ventral appendage, bringing the thecal pore in contact with the stigma. The thecae, particularly those of the small stamens, are effectively stuck to the stigma by the exudate of the latter. The presumed function of this mechanism has yet to be demonstrated experimentally.

### **CYTOLOGY**

Solt and Wurdack (1980) have reported n = 8 for *Monolena dressleri* (*Dressler 4247*), and n = 8 (2n = 16) for plants originating from Cerro Jefe in Panama province (probably *Monolena multiflora*).

My results are as follows: *Monolena dressleri*, n = 8 (*Warner 422*); and *Monolena multiflora*, n = 8(-9?) (*Warner 421*).

### SYSTEMATIC TREATMENT

### Monolena Triana, in Bentham & Hooker, Genera Plantarum. 1(III):756 (1867).

NEOTYPE here designated: Monolena primuliflora Hook. f.

Perennial herbs from a fleshy rhizome; root system fibrous; plants mostly puberulent, and occasionally also with long trichomes on the petiole or blade. Scales of the rhizome opposite and decussate, caducous. Leaves apparently alternate, although opposed by a caducous scale; petiole canaliculate; blades with 3-11 subparallel primary nerves, the nerves either basal (nerved) or suprabasal (plinerved), prominent below. Inflorescence a scorpioid cyme or l-flowered scape. Bracts and scales of the inflorescence mostly caducous, green to white and often translucent, succulent and foliaceous to more often petaloid; scales mostly subulate and often bearing long apical trichomes; floral bracts mostly 2 per flower, occasionally only one for some flowers of the inflorescence, ovate to rarely reniform, entire. Pedicels short. Flowers with a urceolate-campanulate, 10-nerved hypanthium, crowned by a torus that bears the perianth and stamens. Calyx lobes 5, usually fused at the base to form a tube, the lobes mostly triangular, rarely spatulate or emarginate or obcordate, the margin ciliate. Petals 5, free, white to pink, glabrous, obovate to rarely oblong. Stamens 10, glabrous, dimorphic, the antesepalous whorl distinctly larger than the antepetalous whorl; filaments of both whorls dorsiventrally compressed and declined to one side of the flower, white; anthers mostly yellow, linear, 2-celled, tipped with a single, ventrally-inclined terminal pore; connective prolonged, geniculate, usually dorsally tuberculate between the thecae and the insertion of the filament, further extended basally to form a large appendage on the antesepalous stamens and a small appendage on the antepetalous stamens. Ovary 1/2-3/4 inferior, glabrous, obconic, trigonous and trilocular, with axile placentation. Style immersed at base in an ovarial collar, inflated near the middle, slightly contracted and curved below the capitate, papillate stigma. Ovules numerous, borne on narrow, deltoid placentae that intrude into the locule. Fruit a triquetrous capsule, dehiscing by 3 apical valves. Seeds obconic-pyramidate, the surface inconspicuously roughened to papillate.

### KEY TO THE CENTRAL AMERICAN SPECIES OF MONOLENA

- 1. Leaves with all the primary veins diverging from the base of the blade (see Fig. 2B) or with the uppermost pair of primary veins diverging from the midrib within 1/10 the distance from the base to the apex of the blade; flowers 2–8 (–10) per inflorescence.
  - 2. Pedicels 4–6 × 0.5–0.8 mm; petals 24–33 mm long; petioles mostly drying round or nearly so, and brittle; plants glabrous except for minute, scant cilia along the margins of leaves and calyx lobes. . . . . . 4. Monolena morleyi
  - 2. Pedicels 2–3 × 0.8–1.2 mm; petals 11–24 mm long; petioles usually drying flat, flaccid or firm, but not brittle; plants minutely puberulent on underside of the leaves, pedicels and hypanthium.

    - 3. Plants usually epiphytic on tree trunks and logs or terrestrial, occasionally lithophytic; petals 15–24 mm long, pink to white suffused with pink or rarely all white; plants to 55 cm; peduncle and axis of the inflorescence in fruit 19–45 cm measured to the furthest pedicel.

      - 4. Leaves ovate to lanceolate or elliptic, cuneate to obtuse at the base; dried blades subcoriaceous, green to brown above, red to green and often dark brown-red along the veins below; Panama and South America.

        7. Monolena primuliflora

- 1. Leaves with the uppermost pair of primary veins diverging from the midrib 1/5 to 1/3 the distance to the apex of the blade (see Fig. 3B); flowers 2–35 per inflorescence.
  - 5. Flowers (7–) 12–35 per inflorescence.
    - 6. Leaves ovate to nearly round; pedicels and hypanthium glabrous. . . . . . . . 6. *Monolena panamensis*
    - 6. Leaves elliptic to lanceolate or ovate; pedicels and hypanthium minutely puberulent.
      - 7. Flowers (9–) 14–16 (–26) per inflorescence; calyx lobes (3–) 4–7 mm long, emarginate to broadly obovate; ventral appendage of antesepalous stamens geniculate and pointed. . . . . . . . 2. *Monolena grandiloba*
  - 5. Flowers 2–8 per inflorescence.

### 1. Monolena dressleri R. H. Warner, sp. nov.

Figure 2

TYPE: PANAMA, Panamá, El Llano-Cartí highway, ca. 12–14 km N of El Llano, 350–400 m; 9 January 1973; leaves reddish green above, wine red beneath; *R. L. Dressler 4247* (holotype: US!; isotype: PMA!).

Laminae ovatae, basi cordata usque raro obtusa, nerves vel infirme plinerves; inflorescentia floribus (2–) 3–6; bracteae florales obovatae; petala 11–17 mm longa; appendices ventrali selliformes staminum antesepalum.

Epiphytes on low branches and trunks, and on logs and rocks, or terrestrial. Dried rhizomes  $1-7 \times$ 0.6-1.1 (-2.5) cm. Leaves membranaceous when dry, scantily puberulent throughout, the hairs 0.3–0.5 mm long; petioles red to purple, 2–9 cm long; upper blade surface with a metallic luster, dark green to reddish green, turning light green on drying; blades 5.5–16 × 3.5–10.5 cm, ovate, cordate to rarely obtuse at the base, acute to obtuse at the apex, weakly 3-5 (-7) plinerved, the innermost pair of primary veins diverging from the midrib in an opposite arrangement less than 1/10 of the distance to the apex; primary veins prominent below; margin ciliolate-serrulate and often dentate-crenate, occasionally repand, the hairs 0.3–0.5 mm long and 20–30/cm. Inflorescence bearing (2–) 3–6 flowers; peduncle and axis of the inflorescence pink to purple throughout or green toward the apex, together 6.5-13 cm long in flower and 9-18 cm long in fruit when measured to the furthest pedicel, scantily puberulent, the hairs ca. 0.1 mm long; bracts and scales of the inflorescence caducous, translucent white to pale green, petaloid, scantily puberulent on both surfaces, the hairs ca. 0.1 mm long; scales 4, subulate to spatulate to obovate, acute to rounded at the apex, entire to ciliolate-fimbriate with hairs to 1 mm long on the margin; lower and lateral floral bracts each one per flower, all floral bracts 9–11.5 (-15) × 5.0-7.5 mm, obovate, rounded at the apex, entire. Pedicels ca. 2 mm long. Hypanthium ca. 3 mm long, ca. 3.5 (-4.5) mm wide at the torus. Calyx tube absent or to 0.3 mm long; calyx lobes 1.8-2.0 mm long, 1.8-2.5 mm wide at the base, triangular to oblong, acute to rounded at the apex. Pedicel, hypanthium, and the calyx scantily puberulent, the hairs ca. 0.1 mm long. Petals white, 11–17 × (5-) 7.5-10.5 mm, oboyate, rounded at the apex, entire. Antesepalous stamens: filaments 4.3-5.0 mm long; thecae yellow, 1.7-2.0 mm long; connective yellow, extended 1.0-1.5 mm between the thecae and the insertion of the filament, bearing a dorsal tubercle 0.2-0.3 mm long and a saddle-shaped ventral appendage 0.8–0.9 mm long. Antepetalous stamens: filaments (3.2–) 3.6-3.9 mm long; thecae yellow, 1.7-2.0 mm long; connective extended 0.6-1.0 mm between the thecae and the insertion of the filament, the ventral appendage 0.2-0.3 mm long. The connective in both whorls of stamens bending in late anthesis to bring the thecal pore in contact with the stigma.



FIGURE 2. Monolena dressleri R. H. Warner. A. habit; B. leaf blade (abaxial surface); C. inflorescence (fructescence); D. floral bract; E. flower; F. hypanthium and calyx; G. flower (parts removed); H. antesepalous stamen; l. antepetalous stamen; J. fruit; K. valve cover from fruit; L. seeds. (A, B, L from Almeda 6509; C, J, K from Antonio 1265; D-I Dressler 4247).

Ovary ca. 2.0 mm long; style 6.0–6.5 mm long, ca. 1.0 mm wide where expanded. Fruit 1.1–1.2 cm wide. Seeds ca.  $0.7 \times 0.6 \times 0.5$  mm.

DISTRIBUTION AND PHENOLOGY. — This species is known only from the vicinity of the type locality, from 330 m to 500 m elevation near the border between the province of Panamá and the Comarca of San Blas. Flowering collections have been made in February, March, May and August and fruiting collections in January February, March, August and December.

PARATYPES. — PANAMA. Panamá: El Llano-Cartí Rd., 9.6–16 km N of El Llano: Antonio 1265 (CAS), Almeda et al. 6509 (CAS), Busey 380 (MO, US), Croat 33738 (PMA), Folsom & Kauke 1414 (MO), Kennedy et al. 2407 (L, MO), Kennedy & Dressler 2910 (MO), Liesner 1209 (MO), Mori & Kallunki 6394 (MO), Nee et al. 8761 (MO), Nee et al. 9358 (MO, PMA), Systma & Anderson (MO), Warner 411, 412, 414, 415, and 422 (all at MIN); San Blas: Nusagandí, El Llano-Cartí Rd.: de Nevers & González 3660 (CAS, MO, PMA), van der Werff 7011 (CAS, MO, US).

DISCUSSION. — The Panamanian *M. dressleri* is distinguished from all of its South American allies in the *Cordifolia* complex by its slightly larger size and greater number of flowers; and from individual species by the blades being more ovate than round, by the absence of long hairs on the upper blade surface, and by the calyx lobes being more triangular than spathulate.

ETYMOLOGY. — The holotype of *M. dressleri* includes plants in fruit that were collected in the field and a packet of inflorescences from plants cultivated in Panama by Robert Dressler. Attached to the sheet is a letter from Dr. Dressler to John Wurdack, dated 27 February 1973, with the following note, "This plant is quite frequent in the area and grows as epiphyte, lithophyte or terrestrial. The plants are quite attractive, and so far it seems to be quite easy to cultivate." Dr. Dressler has collected nearly every species of *Monolena* known from Panama, and his are always among the few collections with well preserved flowers of these difficult to preserve herbs. For these reasons I have named this species in his honor.

### 2. Monolena grandiloba, R. H. Warner, sp. nov.

TYPE: PANAMA, Chiriquí, near Cerro Colorado, ca. 10 miles from Chami camp, 8°35′N, 81°45′W, along ridge trail in forest, ca. 1600 m, 15 April 1986, *G. McPherson 8938* (holotype: MO!).

Laminae ovatae, basi cuneata usque subcordata, valde plinerves; inflorescentia floribus 14–26; bracteae florales rotundae usque reniformes; lobi calycis 4–6 (–7) mm longi, emarginati ab obovati late; petala 26–28 mm longa; appendices ventrali geniculati et acuti staminum antisepalum.

Terrestrial and epiphytic near the base of tree trunks and on rocks in streams. Dried rhizomes  $4-9 \times 0.5-3.0$  cm. Leaves membranaceous, glabrous to scantily glandular puberulent along the secondary veins on the lower blade surface, the hairs ca. 0.1 mm long; upper blade surface green (on drying may turn rusty red along the veins near the base of the blade); lower surface green, sparsely indented-punctate. Petioles 3-27 cm long. Blades  $10-33 \times 4-18$  cm, ovate to elliptic, the base cuneate or truncate to subcordate, the apex acute to caudate, 7-9 (-11) plinerved, the innermost pair of primaries diverging in an opposite arrangment less than 1/4 of the distance to the apex; primary veins prominent below; margin entire and with hairs ca. 0.2 mm long and 5-10/cm. Inflorescence bearing (9-14-16 (rarely to 25) flowers; peduncle and axis of the inflorescence together 22-35 cm long when measured to the farthest pedicel, elongating to 42-48 cm in fruit; peduncle minutely pubescent with hairs ca. 0.1 mm long; bracts and scales of the inflorescence caducous; scales 2-4; lower floral bracts one per flower, lateral floral bracts apparently 1/2 the number of lower floral bracts; floral bracts obovate  $1.0-1.5 \times 0.6-1.0$  cm. Pedicels 2-4 mm long and 1.2-1.8 mm wide. Hypanthium 5-6 mm long, 6 mm wide at the torus. Pedicels and hypanthium pubescent. Calyx tube 0.8-1.0 mm long; calyx

lobes (3.0-) 4–7 mm long, (3.0-) 4.0–6.0 mm wide at the broadest, obcordate, the margin minutely ciliate. Petals white to bright pink,  $1.4-2\times2$  cm, obovate, rounded at the apex, entire. Antesepalous stamens: filament 4.5–5.0 mm long; thecae yellow, 3.5-3.8 mm long; connective yellow with the ventral appendage and dorsal surface black on dried material up to and including the tubercle; connective extended 2.0–2.4 mm between the thecae and the insertion of the filament, bearing a dorsal tubercle ca. 0.2-0.4 mm long, and a ventral appendage 1.0-1.2 mm long, geniculate and pointed. Antepetalous stamens: filaments 3.8-4.6 mm long; thecae yellow, 3.0 mm long; connective yellow, extended 1.5 mm between the thecae and the insertion of the filament, the ventral appendage 0.5-0.6 mm long. Ovary 3.0-3.2 mm long; style 7-9 mm long, 1.0 mm wide where expanded. Fruits (immature) 1.3 cm wide. Seeds not available.

DISTRIBUTION AND PHENOLOGY. — Monolena grandiloba is endemic to Panama, where it is found in the vicinity of the type collection at an altitude of 1500–1600 m along the continental divide between Chiriquí and Bocas del Toro and Veraguas from 400–1350 m in forests and along streams crossing the road between Alto Piedra and Calovébora and up to the ridges of Cerro Tute. This species has been collected in flower in March, April, May and June and in fruit in March, April and June.

PARATYPES. — PANAMA. Chiriquí: Cerro Colorado Mine, near higher elevation camp, 1,500 m, *Antonio 4867* (MO); along continental divide road 13–15 km beyond intersection in Hato Chami, *Gómez & Warner 511* (PMA); Veraguas: Cerro Tute, ca. 10 km NW of Santa Fe, 800–1350 m. *Antonio 3950* (MO), *Folsom & Edwards 3362* (CAS), *Knapp & Dressler 5424* (CAS, MO), *Mori 6741* (MO); in forest and along streams crossing road between Alto Piedra and Calovébora, 400–900 m, *Croat 27458* (MO, PMA), *Dressler 4998* (US 2 sheets), *Nee 11236* (MO).

DISCUSSION. — *Monolena grandiloba* is distinguished from the other species of *Monolena* by its floral bracts ovate and not enclosing flower in a sac; flowers 5–15 (rarely to 25); calyx lobes broadly obovate, typically 4–7 mm long and 4.0–6.0 mm at the widest; and stamen appendage pointed, sometimes geniculate and often black on dried material.

This species is apparently related to *Monolena multiflora*, based on the large number of flowers relative to other species of *Monolena*, the pubescence on the hypanthium and calyx lobes, and the emarginate to obcordate calyx lobes.

ETYMOLOGY. — The specific epithet refers to the lobes at the end of each calyx segment. On some specimens the calyx segments are so broadly obcordate that pressed on herbarium sheets the lobes look like a pair of mouse cars.

### 3. Monolena guatemalensis Donn. Sm. Bot. Gaz. 42:294. 1906.

TYPE: GUATEMALA, Alta Verapaz, trail from Senjú to Actalá, moist bank along trail; succulent, flowers pink; 17 January 1905. *William R. Maxon & R. Hay 3331* (Lectotype designated here: US!).

Epiphytes high in trees, on stumps, or terrestrial. Dried rhizomes (4-) 6.5–15 × 0.7–2.0(–3.0) cm. Petioles (2.5-) 4–24 cm long; fresh blades "fleshly-membranous, rich green with prominent areolations above, purplish-orchis or suffused with pale silvery-green beneath" (*Steyermark 41922*); dried blades membranous, light green below and dark green above, (6.5-) 8–33 × (2.4-) 5–21 cm, ovate, cordate at the base, acute to subacuminate at the apex, with entire or sometimes crenate margins, weakly 5–7 (–9) plinerved, the innermost pair of primary veins diverging from the midrib in an opposite arrangement in the lower 1/10 of the blade, the primary veins prominent below; leaves puberulent throughout with hairs 0.2–0.3 mm long, the margin with hairs 0.3–0.5 mm long and ca. 4–20/cm. Inflorescence bearing 3–7 flowers; peduncle and axis of the inflorescence together 12–20 cm long in flower and 19–33 cm long in fruit when measured to the furthest pedicel, scantily puberulent with hairs ca. 0.2 mm long; bracts and scales of the inflorescence caducous, petaloid, en-

tire, scantily puberulent on both sides with hairs ca. 0.1 mm long; scales 4,  $7-12 \times (2-)$  3–5 mm, subulate to obovate and rounded at the apex, occasionally with a few hairs near the apex; lower floral bracts one per flower; lateral floral bracts 2, these approximately opposite the 2 lowermost flowers; all floral bracts (6-)  $10-15 \times (3-)$  7–10 mm, obovate, rounded at the apex. Pedicels 2–3 mm long. Hypanthium ca. 3.5 mm long, 3.5-4.5 mm wide at the torus. Calyx tube 0.1-0.2 (-0.5) mm long; calyx lobes 1.5-2.3 mm long, 2.0-2.2 mm wide at the base, triangular, rounded at the apex. Pedicel, hypanthium, and margin and both sides of the calyx lobes scantily puberulent with hairs ca. 0.1 mm long. Petals pink,  $22-24 \times 13-20 \text{ mm}$ , obovate, rounded at the apex, entire. Antesepalous stamens: filaments 4.0-4.5 mm long; thecae ca. 3 mm long; connective extended 1.0-1.3 mm between the thecae and the insertion of the filament, bearing a dorsal tubercle ca. 0.2 mm long and a subglobose ventral appendage 0.7-0.9 mm long. Antepetalous stamens: filament 3.2-4.0 mm long; thecae ca. 2.7 mm long; connective extended ca. 1 mm long between the thecae and the insertion of the filament, the ventral appendage 0.2-0.3 mm long. Ovary ca. 2.5 mm long; style 6.0-6.5 mm long, 0.3-0.6 mm wide where expanded. Fruit ca. 1.4 mm wide. Seeds ca.  $1.1 \times 0.6 \times 0.4 \text{ mm}$ .

DISTRIBUTION AND PHENOLOGY. — This species is endemic to Guatemala and is disjunct by ca. 900 km from its nearest congener in Costa Rica, so far as is now known. It occurs in central Guatemala at (300–) 900–1500 m elevation. *Monolena guatemalensis* has been collected in flower in January, April and May, in fruit in January and March.

ADDITIONAL SPECIMENS EXAMINED. — GUATEMALA. Alta Verapaz: Secanquim, trail to Secoyocta, *Goll 158* (US); vicinity of Sepacuite, *Cooks & Doyle 32* (US); near the finca Sepacuite, Se Shun, *Cook & Griggs 106* (Syntype: US); near finca Sepacuite, *Cook & Griggs 515* (Syntype: US); Between Sepacuite and Sicanquim, *Pittier 314* (Syntypes: US & NY, photos at GH & MO); Quiché: Cerro Putul, "Zona Reyna," *Skutch 1826* (F, GH, NY, US); Izabal: Cerro San Gil, *Steyermark 41922* (F, NY, US 2 sheets).

DISCUSSION. — The lectotype designated here was selected because it has the best preserved flowers of the specimens cited by Donnell Smith in the protologue. However, the petioles are somewhat longer than typical.

Monolena guatemalensis is distinguished by a combination of characters not seen elsewhere in the genus. The blades are ovate, nerved to slightly plinerved, and lacking sclereids as in members of the Cordifolia complex. However, these plants differ from those of the Cordifolia complex by their larger size, fewer lateral floral bracts relative to the number of flowers, and antesepalous stamens with a subglobose ventral appendage. The shape of the staminal appendages and the low number of floral bracts suggest a relationship to M. panamensis. The overall pubescence of M. guatemalensis is of slightly longer hairs than typical for the genus.

### 4. Monolena morleyi R. H. Warner, sp. nov.

TYPE: PANAMA, Coclé, 7 km north of El Copé, Forgotten Hill, area surrounding Rivera Sawmill; 650–850 m; 5 Nov 1977; epiphytic herb, petals pink, stamens yellow; *J. P. Folsom 6204* (holotype: US!; isotypes: CAS! and MO!).

Plantae glabrae; laminae ovatae usque fere rotundae, basi cordata, nerves vel infirme plinerves; inflorescentia floribus 4–8 (–10); bracteae florales obovatae; pedicelli florum 4–6 mm tenues; petala 24–33 mm longa; appendices ventrali subglobosi staminum antisepalum.

Epiphytic herbs. Dried rhizomes  $4-10 \text{ cm} \times 1-2 \text{ cm}$ . Leaves glabrous; petioles nearly round and brittle when dried, deeply caniculate, red, turning red-brown on drying, 4-13 cm long; blades  $7-20 \times 6-17 \text{ cm}$ , ovate, cordate and sometimes oblique, subcaudate to acute at the apex, subcoriaceous,  $7-9 \times 6-17 \text{ cm}$  ovate, cordate and sometimes oblique, subcaudate to acute at the apex, subcoriaceous,  $7-9 \times 6-17 \text{ cm}$  ovate, cordate and sometimes oblique, subcaudate to acute at the apex, subcoriaceous,  $7-9 \times 6-17 \text{ cm}$  ovate, cordate and sometimes oblique, subcaudate to acute at the apex, subcoriaceous,  $7-9 \times 6-17 \text{ cm}$  ovate, cordate and sometimes oblique, subcaudate to acute at the apex, subcoriaceous,  $7-9 \times 6-17 \text{ cm}$  ovate, cordate and sometimes oblique, subcaudate to acute at the apex, subcoriaceous,  $7-9 \times 6-17 \text{ cm}$  ovate, cordate and sometimes oblique, subcaudate to acute at the apex, subcoriaceous,  $7-9 \times 6-17 \text{ cm}$  ovate,  $7-9 \times 6-17 \text{ cm}$ 

(-11) -nerved, to slightly plinerved, the innermost pair of primary veins diverging from the midrib in an opposite arrangement up to 1/10 of the distance to the apex; primary veins very prominent below, raised into prominent ridges near the base of the blade; margin faintly ciliolate-serrulate, the hairs 0.5–1.5 mm long and 5–8/cm; on drying the upper blade surface dark red-tan to green, the lower surface indented-punctate, tannish green to brown and with the veins red-brown. Inflorescence with 4-8 (-10) flowers; peduncle pink, wiry when dried, peduncle and axis of the inflorescence together 15-22 cm long in flower and 32 cm in fruit when measured to the furthest pedicel, glabrous; scales (2–) 4, white; lower floral bracts one per flower, the lateral floral bracts approximately half as many as the lower floral bracts, all floral bracts 1.7–2.2 × 1.1–1.8 mm, obovate, rounded to emarginate at the apex, entire. Pedicels 4–6 mm long, 0.5–0.8 mm wide at the narrowest point. Hypanthium 3–4 mm long, 4.0-4.5 mm wide at the torus. Calyx white; calyx tube 0.4-0.8 mm long; calyx lobes 2.5–2.7 mm long, 2.2–2.5 mm wide at the base, triangular and rounded at the apex to oblong with the apex truncate to rarely emarginate; margin of the calyx lobes scantily ciliolate with hairs ca. 0.1 mm long, the pedicels, hypanthium and calyx otherwise glabrous. Petals white, pink or lavender, 24–33 × 24 mm, obovate, rounded at the apex, entire. Antesepalous stamens: filaments 4.0-4.8 mm long; thecae yellow, 2.4–3.0 mm long; connective extended 1.2–2.0 mm between the thecae and the insertion of the filament, bearing a dorsal tubercle 0.2 mm long and a subglobose ventral appendage 1.0-1.2 mm long. Antepetalous stamens: filaments 3.8-4.0 mm long; thecae yellow, 2.0-2.5 mm long; connective extended 1.0-1.2 mm between the thecae and the insertion of the filament, the ventral appendage 0.3-0.6 mm long. Ovary ca. 2.0 mm long; style 5.0-7.0 mm long and ca. 0.8 mm wide where expanded. Fruits 1.3–1.4 mm wide. Seeds ca.  $0.8 \times 0.8 \times 0.5$  mm.

DISTRIBUTION AND PHENOLOGY. — *Monolena morleyi* is endemic to Panama, where it is known only from the vicinity of El Copé in the province of Coclé. It grows in cloud forest from 700–1300 m elevation, including the wind-swept ridge along the continental divide. Flowering material has been collected in September, October, November, February and April. Fruiting plants have been collected in January.

PARATYPES. — PANAMA. Coclé: continental divide above El Copé, region of Alto Calvario and El Potroso (Rivera) sawmill, *Croat 44681* (MO), *Croat 67561* (MO), *Folsom & Collins 1537* (MO), *Folsom & Collins 6535* (MO), *Hammel 2427* (MO), *McPherson 7673* (MO), *Sytsma 1815* (MO).

DISCUSSION. — This species of *Monolena* is unique in the genus for being entirely glabrous; petioles brittle on dried material; pedicels longer and more delicate than other species of *Monolena*, and having the largest petals in the genus. *Monolena morleyi* is most closely related to *M. panamensis*. Both species have ovate to cordate leaves; glabrous pedicels and hypanthium; long pedicels relative to other species of *Monolena*; large floral bracts that only partially envelop the flower buds; and large, showy flowers. The two species are distinguished by the unique characters of *M. morleyi* mentioned above and the larger number of flowers per inflorescence of *M. panamensis*.

While leaves of this species were not cleared, based on the texture, color and surface features of the leaf blade are similar to *M. multiflora*; thus I suspect that foliar sclereids are abundant and associated with the lower hypodermis, and possibly with the upper hypodermis as well.

ETYMOLOGY. — This species is named for the late Dr. Thomas Morley, an expert on the genera *Mouriri* and *Votomita* (Melastomataceae), dedicated conservationist, and teacher of plant taxonomy to generations of students at the University of Minnesota.

## **5.** *Monolena multiflora*, R. H. Warner, sp. nov. Figure 3

TYPE: PANAMA, Panamá, La Envida, region of Cerro Jefe; flowers pale pink; 18 April 1971; R. L. Dressler & N. H. Williams 3950 (holotype: US 2849129!; isotypes: MO!, PMA!, US 2849130!).

Laminae ellipticae usque ovatae, basi cuneata usque obtusa, valde plinerves; inflorescentia floribus (15–) 20–35; bracteae florales rotundae usque reniformes; petala (10–) 15–29 mm longa; appendices ventrali subglobosi staminum antisepalum.

Epiphytes on tree trunks and low branches, and on stumps and rocks. Dried rhizomes 3.0–8.0 × 0.6-2.0 cm. Plants mostly glandular puberulent, the hairs most conspicuous on the margin of the leaf blade and along the veins on the lower blade surface; hairs 0.3-0.5 mm long and mostly ca. 30/cm along the blade margin, elsewhere 0.1–0.2 (–0.3) mm long; petals, androecium, gynoecium and fruit glabrous. Leaves subcoriaceous; upper blade surface green, often turning red-brown on drying; lower surface rarely green throughout, mostly red, particularly along the veins, turning green with dark brown to red veins and often becoming indented-punctate on drying. Petioles red, 4-20 cm long; blades 14-30 × 3.5-18 (-23) cm, elliptic to ovate-lanceolate, cuneate to obtuse and often decurrent at base, acute to acuminate at apex, strongly 5–7 (–9) plinerved, the innermost pair of primaries diverging in an alternate to rarely opposite arrangement from (rarely 1/10) 1/5 to 1/3 of the distance to the apex; primary and occasionally secondary veins sunken above and prominent below; margin ciliolate-serrulate and sometimes repand. Inflorescence bearing (15-) 20-35 flowers; peduncle and axis of the inflorescence red and succulent, together 10.5-43 cm long when measured to the farthest pedicel, often bearing both flowers and fruit; bracts and scales of the inflorescence caducous, translucent pink to white or green; scales 4(-6),  $8-12 \times 4-8$  mm, obovate, rounded at the apex, the margin entire or occasionally ciliate near the apex, the hairs ca. 0.3 mm long; lower floral bracts one per flower, lateral floral bracts approximately half as many as the lower floral bracts, all floral bracts 9.5–16 × 9.0–16 mm, broadly obovate to round or reniform, rounded to emarginate at the apex, strongly concavo-convex, entire; the floral bracts form a pouch that envelops the flower buds until shortly before the flowers open. Pedicels 0.5-2.0 mm long, 0.8-1.5 mm wide. Hypanthium green or pink, 2.5–4.2 mm long, 3.0–4.0 (–5.0) mm wide at the torus. Calyx tube 0.3–0.6 mm long; calyx lobes green to pink, 1.6–2.5 (–3.0) mm long, 2.0–2.5 mm wide at the base, ranging from triangular with a central ridge that terminates just below the apex, to truncate, emarginate or slightly obovate. Petioles, hypanthium and calyx scantily puberulent. Petals white to cream or pink and often with translucent veins, (10-) 15-20 × (6-) 8-11 mm, obovate to oblong, rounded at the apex, entire. Antesepalous stamens: filament 3.4–4.5 (–5.0) mm long; thecae yellow, 2.3–3.0 mm long; connective entirely yellow, or (in Colón and Coclé) bicolored with the ventral appendage and dorsal surface pink up to and including the tubercle; connective extended 1.2-1.5 (-2.1) mm between the thecae and the insertion of the filament, bearing a dorsal tubercle ca. 0.1–0.2 mm long, and a subglobose ventral appendage 0.6–0.8 (-1.3) mm long. Antepetalous stamens: filaments 3.1–3.6 mm long; thecae yellow, 2.0–2.4 mm long; connective yellow, extended 0.8–1.0 mm between the thecae and the insertion of the filament, the ventral appendage 0.2-0.3(-0.5) mm long. Ovary 3.0-3.2 mm long; style (5.0-) 5.5-6.5 mm long, 0.7-1.7 mm wide where expanded. Fruits 1.2-1.5 cm wide. Seeds ca.  $0.8 \times 0.5 \times 0.4$  mm.

DISTRIBUTION AND PHENOLOGY. — *Monolena multiflora* is endemic to Panama. East of the Panama Canal it occurs in Panamá province from 1000 m in the Cerro Jefe region east to the area where the provinces of Panamá and Colón border San Blas at elevations of 400–500 m and in Colon from 600 m in the Santa Rita Ridge area to near sea level along the Río Guanche. West of the Panama Canal,

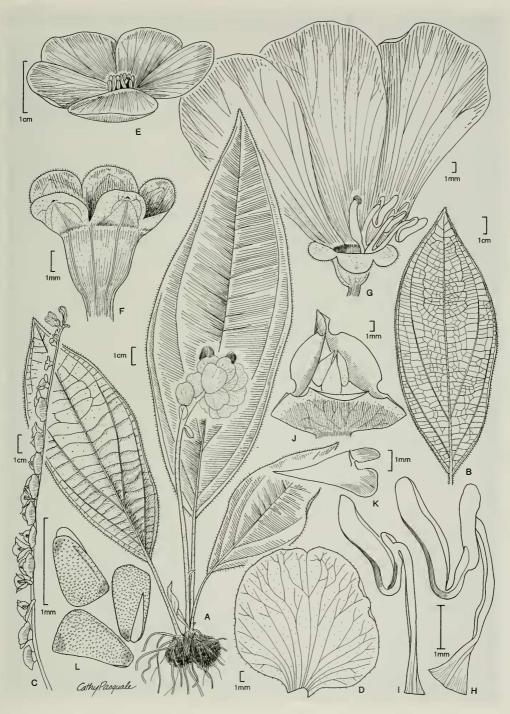


FIGURE 3. Monolena multiflora R. H. Warner. A. habit; B. leaf blade (abaxial surface); C. inflorescence (primarily with fruits); D. floral bract; E. flower; F. hypanthium and calyx; G. flower (parts removed); H. antesepalous stamen; I. antepetalous stamen; J. fruit; K. valve cover from fruit; L. seeds. (A, B from Dressler 4132; C, J-L from Sytsma et al. 2471.; D-l from Dressler 4251.)

*M. multiflora* occurs in Coclé from 800 m near Cope to less than 100 m near Coclé Del Norte in Colón. This species has been collected in fruit and flower every month of the year.

PARATYPES. — PANAMA. Coclé: continental divide between Llano Grande and Cascajal, Knapp 1966 (CAS, PMA), Sytsma et al. 4422 (MO), 4393 (CAS), Sytsma 3846 (CAS), Sytsma 3903 (CAS); continental divide N of Penonomé, road to Coclesito, Antonio 3068 (CAS), Croat 49239 (CAS), D'Arcy & Hammel 12284 (CAS, MO), Hammel 1630 (CAS, MO), Hammel 7211 (MIN), Churchill et al. 4155 (CAS, PMA); between Río Blanco and Caño Sucio, Davidse & Hamilaton 23623 (PMA), Sytsma et al. 2471 (CAS), Antonio 3674 (MO); trail from Caño Sucio to waterfall of Río Tife, Knapp 3767 (MO); Atlantic side of continental divide above El Cope, Knapp & Dressler 3462 (CAS); Río San Juan above confluence with Río Tife, Hammel 3445 (CAS); Colón: Coclé del Norte, east of town, Hammel 4514 (MO); 6 km S of Porto Bello, along Río Guanche, 5-20 m, Nee & Gentry 8707 (MO), Kennedy & Foster 2176 (F, MO, NY, US), Foster 2778 (F, MIN, PMA), Warner 427 (MIN), Maas et al. 1576 (F, MO, US), Dressler 4140 (US), Dressler 4242 (US), Dressler 4301 (PMA, US); Río Piedras, Santa Rita Ridge, Antonio 3770 (cultivated material), Antonio 3771 (MO), Hammel 6353 (MO); Río Gatún, Antonio 3827 (MO); south approach to Cerro Bruja from Río Escandaloso, Antonio 1340 (MO), Hammel 3109 (CAS), Hammel 3187 (CAS); Panamá: 6 miles above Goofy Lake on road to Cerro Jefe, Croat 15214 (MO); Cerro Jefe, Correa & Dressler 558 (PMA), Almeda & Nakai 3462 (CAS), Almeda et al. 5832 (CAS), Croat 67071 (CAS, PMA), Dressler 5138 (US), Henslow & McPherson 1003 (PMA), Mori 6519 (MO), Sytsma et al., 2852 (CAS); La Eneida, region of Cerro Jefe, 650 m, Dressler 4132 (PMA, US), 4251 (US); woods around La Eneida, Luteyn & Kennedy 1768 (F, MO); beyond La Eneida, Correa & Dressler 804 (GH, MO, NY, PMA, US); Altos del Río Pacora, Dressler 5287 (PMA), Lewis et al. 2265 (GH, MO); Campo Tres, 3 mi NE of Altos de Pacora, *Liesner 547* (CAS, MO); 5–10 km NE of Altos de Pacora, on ridge top, ca. 600 m, Mori & Kallunki 3422 (MO); San Blas: continental divide 5-10 km west of El Llano-Cartí Road, de Nevers & Herrera 4495 (CAS, MO); Cerro Brewster, de Nevers et al. 4032 (CAS, MO); Yar Bired, continental divide between Cangandí and San José, de Nevers & Herrera 7001 (MO, CAS).

DISCUSSION. — *Monolena multiflora* is distinguished by the leaves ovate to lanceolate or elliptic and strongly plinerved, the large number of flowers (15–35) per inflorescence, and the floral bracts that envelop the buds in a pouch.

There are three distinct populations of *M. multiflora*. Plants from the population east of the Panama Canal in the region of Cerro Jefe east into San Blas are usually distinguishable by leaves turning iron red on drying, presumably related to the abundance of sclereids; plants from this region have the highest density of foliar sclereids of all the specimens examined to date.

In Colón, also east of the canal, *M. multiflora* most often occur as lithophytes along streams and tend to be of smaller stature and with leaf blades narrow and delicate (presumably reflecting the very low density of foliar sclereids recorded from plants in this region). The lithophytic and riverine habitat, smaller stature and more delicate leaves of *M. multiflora* in the Santa Rita Ridge area are characteristics reminiscent of *M. trichopoda*. However, these two species can be distinguished by the larger number of flowers and the ciliolate-serrulate margin of the leaf blades on *M. multiflora*, and by the two rows of trichomes on the petioles of *M. trichopoda*. Specimens from Río Guanche suggest that plants in this particular area rarely set fruit.

West of the Panama Canal, *M. multiflora* is distinguished by strongly decurrent leaf bases and flower buds enclosed in a particularly pronounced pouch formed by the floral bracts. *Monolena multiflora* is sympatric with *M. trichopoda* in the province of Coclé (along the Río Blanco), although their habitats are distinct. *Monolena trichopoda* grows primarily on rocks and logs in and along fast running rivers, but is seldom found in the adjacent forest where *M. multiflora* grows in this region.

ETYMOLOGY. — The specific epithet acknowledges that this species has the most flowers per inflorescence of all *Monolena* species.

### 6. Monolena panamensis R. H. Warner, sp. nov.

TYPE: PANAMA, Coclé, La Mesa, 4 km N of El Valle, 875 m; terrestrial, petals pink; 12 February 1974; *M. Nee & Hale 9638* (holotype: US!; isotype: MO!).

Laminae ovatae usque fere rotundae, basi cordata vel truncata vel raro obtusa et interdum obliqua, modice plinerves; inflorescentia floribus 12–20; bractea florales obovatae; petala (12–)14–24 mm longa; appendices ventrali subglobosi staminum antisepalum.

Epiphytes on tree trunks, or on stumps and logs, or terrestrial. Dried rhizomes  $4-9 \times 0.6-2.0$  cm. Leaves subcoriaceous, rarely glabrous, usually scantily puberulent throughout and most conspicuously so along the veins of the lower surface, the hairs 0.1–0.2 mm long; petioles fleshy, caniculate, red, 6-29 cm long; upper blade surface green and occasionally with the margin red; lower surface light green when fresh, indented-punctate and usually turning tan or rarely pinkish on drying; blades 7.5–23 × 8–23 cm, ovate to nearly round, cordate and sometimes oblique, truncate or rarely obtuse at the base, acuminate to rarely subcaudate at the apex, weakly 5-7 (-9) plinerved, the innermost pair of primary veins diverging from the midrib in an opposite arrangement up to 1/5 of the distance to the apex, or (in plants from Cerro Trinidad) more prominently 9 (-11) plinerved, the innermost pair of primary veins diverging from the midrib in an opposite arrangement up to 1/4 of the distance to the apex, primary veins prominent below; margin apparently entire but actually faintly ciliolate-serrulate, the hairs 0.3-0.5 mm long and 2-4/cm. Inflorescence bearing 12-20 flowers; peduncle and axis of the inflorescence red to purple, succulent, together 15–30 cm long in flower and (15–) 30–42 cm long in fruit when measured to the furthest pedicel, very scantily puberulent with hairs ca. 0.1 mm long; bracts and scales of the inflorescence caducous, translucent green to white, petaloid, very scantily puberulent on the adaxial surface with hairs ca. 0.1 mm long; scales 4, ca. 2.1 × ca. 0.9 mm, obovate, round at the apex, the margin entire and occasionally with a few hairs near the apex, the hairs ca. 0.3 mm long; lower floral bracts one per flower, the lateral floral bracts approximately half as many as the lower floral bracts, all floral bracts  $1.4-1.5 \times 1.0-1.1$  mm, obovate, rounded at the apex, concavo-convex, entire. Pedicels 2-3.5 mm long, 0.8-1.2 mm wide at the narrowest point. Hypanthium 3–4 mm long, 4.0–4.5 mm wide at the torus. Calyx tube 0.4–0.6 mm long; calyx lobes 2.5-2.7 mm long, 2.2-2.5 mm wide at the base, triangular and rounded at the apex to oblong with the apex truncate to rarely emarginate. Margin of the calyx lobes scantily ciliolate with hairs ca. 0.1 mm long, the pedicels, hypanthium and calyx otherwise glabrous. Petals pink to lavender, (12-) 14-24 × 8–10 mm, obovate, rounded at the apex, entire. Antesepalous stamens: filaments 2.8–6 mm long; thecae yellow, 2.2-4 mm long; connective yellow, extended 1.6-2.5 mm between the thecae and the insertion of the filament, bearing a dorsal tubercle 0.2–0.3 mm long, and a subglobose ventral appendage 0.8-1.5 mm long. Antepetalous stamens: filaments 2.6-3.2 (-4.0) mm long; thecae yellow, 2.0–3.0 mm long; connective yellow, extended 1.0–1.4 mm between the thecae and the insertion of the filament, the ventral appendage 0–4–0.5 mm long. Ovary ca. 2.4 mm long; style 5.5–6.0 mm long, and ca. 1.0 mm wide where expanded. Fruits 1.1–1.2 mm wide. Seeds ca.  $0.8 \times 0.8 \times 0.5$  mm.

DISTRIBUTION AND PHENOLOGY. — *Monolena panamensis* is endemic to Panama. Typical plants are found in the mountains north of El Valle de Antón, Coclé, from 800–1100 m elevation. A distinct sort of *Monolena panamensis* is known only from Cerro Trinidad, province of Panamá, at 950 m elevation. Flowering collections have been made in every month except August and October, fruiting collections from January through September.

PARATYPES. — PANAMA. Coclé: along road to and in forest at La Mesa, 2.8–3.4 miles NW of El Valle de Antón, *Correa et al. 4245* (PMA), *Luteyn 4069* (F); La Mesa, *Warner 404* through *Warner 410* (MIN); La Mesa, ca. 2 km W of Cerro Pilón, *Croat 37432* (MO), *de Nevers et al. 6339* (CAS, MO); *Sullivan 505* (CAS, MO); Cerro Pilón, ca. 5 km NE of El Valle, *Croat 14346* (F, MO NY),

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Dwyer et al. 4481 (MO), Dwyer & Lallathin 8597 (NY), Kirkbride 1072 (MO-2 sheets, NY), Liesner 770 (MO), Mori et al. 6570 (MO, US); hills N of El Valle de Antón, Dressler 4081 (US-2 sheets), Hamilton et al. 4124 (MO), Lewis et al. 1773 (MO); Cerro Gaital Caracoral, Croat 67256 (CAS, MO, PMA, US), Duke & Dwyer 15137 (MO), Dwyer & Correa 8840 (MO), Knapp 1063 (CAS, MO, US), Knapp 5309 (CAS), Knapp & Dressler 4899 (CAS), McPherson 11218 (MO), Miller et al. 783 (CAS, PMA, US), Sytsma 3744 (MO), Sytsma 3772 (MO), Sytsma 4070 (CAS); Cerro Pajita, region N of El Valle de Antón, Allen 4494 (MO); Panamá: trail to top of Cerro Pelado, 1,000 m elevation, Antonio 1081 (CAS, MO); Capira, NE side or Cerro Trinidad, 950 m elev., Foster 2118 (F, MIN, MO, PMA, US).

DISCUSSION. — The distinguishing characters of M. panamensis include ovate leaves that are weakly plinerved, the inflorescence with 12-20 flowers, lateral floral bracts half as many as the lower floral bracts, obovate floral bracts, and the glabrous hypanthium. Foliar sclereids are associated only with the lower hypodermis and are moderately abundant in typical plants, but are rare in plants from Cerro Trinidad.

The plants from Cerro Trinidad differ from typical plants in a number of points. In particular, the petioles are mostly longer (to 29 cm) than typical plants (to 16 cm); the leaf blades are rounder and more strongly cordate at the base, have 9 primary veins (compared to 5–7 primary veins in typical plants), and the blades are more prominently plinerved; and the stamens are about 50% larger than in typical plants.

ETYMOLOGY. — The specific epithet acknowledges that this species is endemic to Panama.

### 7. Monolena primuliflora Hook. f., Bot. Mag. 1870:5818 (February 1, 1870).

LECTOTYPE here designated: Plate 5818 in the Botanical Magazine.

Bertolonia primuliflora H. H. Dombrain, Floral Mag. 9:471–472 (1870). Lectotype here designated: Plates 471-472 in the Floral Magazine. The Floral Magazine cannot be specifically dated, but must have been published at about the same time as the Hooker description. In his treatment of Monolena primuliflora Hooker noted that the synonym Bertolonia primuliflora was commonly used among horticulturalists, but he did not mention Dombrain's article.

Epiphytic or terrestrial. Dried rhizomes  $3-9 \times 0.6-3$  cm. Plants mostly glandular-puberulent, the hairs most conspicuous along the blade margin and along the veins on the lower blade surface; hairs 0.1-0.2 mm long, ca. 20/cm along the margin; juvenile leaves occasionally bearing hairs 2.0-2.5 mm long on the adaxial surface. Leaves mostly subcoriaceous, plants from Cerro Matama in Costa Rica are membranous; petioles red to green, 7–20 cm long; upper blade surface green, often turning brown on drying; lower surface red to green often turning dark brown-red along the veins on drying; blades 10-25 cm long, 4-17 cm wide, ovate, lanceolate to nearly elliptical, cuneate to obtuse at the base, acuminate at the apex; blades (3–) 5–7 (–9)-nerved or plinerved, the innermost pair of primary veins diverging from the midrib in an opposite arrangement within 1/10 of the distance to the apex (on plants from eastern Panama and South America), or within 1/5 to 1/3 of the distance to the apex (on plants from the Talamanca Mountains of western Panama and adjacent Costa Rica); primary veins prominent below; margin ciliolate-serrulate; juvenile leaves occasionally bearing hairs 2.0-2.5 mm long on the adaxial surface. Inflorescence bearing 2–6 (–7) flowers; peduncle and axis of the inflorescence red, succulent, together 6-19 cm long in flower and 27-45 cm long in fruit when measured to the furthest pedicel; scales of the inflorescence 2 or 4, 7–12 × 1.5–5.0 mm, subulate to elliptic to obovate, acute to rounded at the apex, entire and occasionally with a few marginal hairs 0.3-0.8 mm long; lower and lateral floral bracts each one per flower, all floral bracts 10–20 mm long (10–16 mm long on plants from eastern Panama, 16–20 mm long on plants from western Panama and Costa Rica),

(5–) 9–14 mm wide, obovate, rounded at the apex, concavo-convex, entire. Pedicels 2–3 mm long. Hypanthium 2.5–3.5 (–5.0) mm long, 3–4.5 mm wide at the torus. Calyx tube 1.5–4.0 mm long, calyx lobes 1.5–3.0 mm long, 2.5–3.2 mm wide at the base, triangular to oblong, rounded to emarginate at the apex. The pedicel, hypanthium and calyx scantily puberulent, the hairs ca. 0.1 mm long. Petals white to pink or purple,  $15-24\times12-15$  mm, obovate, rounded at the apex, entire. Antesepalous stamens: filaments 3.5–5.0 mm long; thecae yellow, 2.0–2.5 mm long; connective yellow, extended 1.0–1.5 mm between the thecae and the insertion of the filament, bearing a dorsal tubercle 0.1–0.2 mm long and a subglobose ventral appendage 0.8–1.2 mm long. Antepetalous stamens: filaments 2.8–4.2 mm long; thecae yellow, 1.6–1.9 (–2.3) mm long; connective yellow, extended 0.6–1.0 mm between the thecae and the insertion of the filament, bearing a dorsal tubercle ca. 0.1 mm long and a subglobose ventral appendage 0.3–0.5 mm long. Ovary ca. 2.4 mm long; style (3.5–) 6.0–7.0 (–7.8) mm long, ca. 1.8 mm wide where expanded. Fruit 1.5–1.7 cm wide. Seeds ca.  $0.9\times0.5\times0.4$  mm.

DISTRIBUTION AND PHENOLOGY. — This is the most wide-ranging species of *Monolena*. It occurs from eastern Costa Rica to southern Peru and adjacent Brazil (Acre), at elevations ranging between 300–1900 meters. In Central America *M. primuliflora* has been collected in flower and fruit from January through August.

ADDITIONAL SPECIMENS EXAMINED. — COSTA RICA. Limón: Asunción, Río Segundo, 300-600 m, Gómez et al. 23426 (CAS, MO, US), Gómez & Herrera 23472 (CAS, US). PANAMA. Bocas del Toro: continental divide trail near Fortuna Dam, 1200-1300 m, Almeda et al. 6257 (CAS); Continental Divide above Quebrada Arena, Carretera del Oleoducto, IRHE Fortuna Hydroelectric Project, Churchill et al. 4698 (CAS), Knapp & Vodicka 5671 (CAS, MO); Chiriquí: highway between Gualaca and Chiriquí Grande, just south of continental divide trail, Croat 66834 (CAS, US), 10 km N of Los Planes de Hornito, near IRHE Fortuna Hydroelectric Project, Antonio 5180 (CAS), Churchill 5251 (CAS), Correa 2143 (US), Gordon 300 (CAS), Knapp 5023 (CAS, MO), Mendoza 327 (US), Valdespino et al. 558 (PMA). San Blas: Cerro Habú, 1,400-2,500 ft., Sytsma et al. 2668 (MO), Sytsma et al. 2745 (CAS, MO). Darién: Cerro Pirre, 750-1560 m elev.; Gentry & Clewell 6956 (MO), Duke 6083 (GH, MO), Duke 5342 (MO), Duke 6597 (MO), Duke & Ellias 13815 (MO), Duke & Ellias 13794 (MO), Bristan 539 (MO), Croat 37870 (MO), Folsom 4248 (CAS, MO), Folsom et al. 4468 (CAS, MO, PMA); ridge from Altos de Nique to Cerro Pirre, Croat 37842 (MO), Cana and vicinity, 2000-6500 ft., Williams 812 (US, NY); Cuasi-Cana trail between Cerro Campamiento and La Escalera to "Paramó," east of Tres Bocas, Kirkbride & Duke 1344 (MO, NY); Crest Cana Cuasi Trail, Real District, Terry & Terry 1543 (F, GH).

DISCUSSION. — Monolena primuliflora Hook.f. was the first species of Monolena described, that having been done in 1870. Hooker's (1870) descriptions and plate of M. primuliflora in the Botanical Magazine and the plate and description of Bertolonia primuliflora in the Floral Magazine (Dombrain 1870) were apparently published at about the same time. The Hooker description was published in February while the Dombrain article cannot be specifically dated. Both descriptions are discussed in the March 1870 volumes of Gardener's Chronicle (Anonymous 1870, Anonymous 1870a).

The description and plate in the Botanical Magazine were prepared from plants cultivated in England from plants originally introduced by Wallis from the Rio Zamora, Ecuador (Anonymous 1870, Anonymous 1870a). No herbarium voucher for these is known. The specific epithet has usually been spelled "primulaeflora." This is corrected here to "primuliflora," in accordance with Art. 60.8 of the ICBN (Greuter et al. 2000)

This species is distinguished by a combination of characters, the most important being leaves that are ovate to elliptic, cuneate to obtuse or rarely subcordate at the base, and nerved to only slightly plinerved (except for plants from the Talamanca Mountains of Costa Rica and Panama with strongly plinerved leaf blades) and an inflorescence typically bearing 3–6 flowers. Variation within this spe-

cies is considerable, particularly in the Talamanca Mountains, at lower elevations along the Pacific coast of Colombia and Ecuador, and in Acre, Brazil.

In *M. primuliflora* foliar sclereids are typically moderately abundant in the lower hypodermis. However, plants at low elevations along the Pacific lowlands of Colombia have a very low density of foliar sclereids. Apparently following this pattern, plants from low elevations (300–400 m) in Costa Rica have membranous leaves, suggesting a low density of foliar sclereids.

### 8. Monolena trichopoda R. H. Warner, sp. nov.

TYPE: PANAMA, Veraguas, NW of Santa Fe, 2.7 km from Escuela Agrícola Alto de Piedra on road to Calovébora; on rocks along stream; corolla white, flushed with pink; 30 March 1975; *S. Mori & J. Kallunki 5335* (holotype: MO!; isotype: US!).

Laminae elliptico-lanceolatae, basi cuneata usque obtusa, valde plinerves; petioli setosi, setae ephemerae in series duas; inflorescentia floribus 3–5 (–8); bractae florales ellipticae usque anguste obovatae; petala 11–16 (–18) mm longa; appendices ventrali linguiformi staminum antisepalum.

Epiphytes on low branches, and on logs and rocks. Dried rhizomes  $1-4 \times 0.3-1.0$  cm. Leaves membranaceous when dry, puberulent throughout, the hairs ca. 0.1 mm long; juvenile leaves occasionally bearing hairs 2.0–2.5 mm long on the adaxial surface; petioles purple, 2–12 (–15) cm long, bearing two rows of setae 0.9-2.5 (-3.0) mm long along the lateral ridges; upper blade surface green; lower surface purple, often turning red in the areoles and yellow-green along the primary and the secondary veins on drying; blades  $7-22.5 \times 2.0-10$  cm, elliptic-lanceolate, cuneate to obtuse at the base, acute to subacuminate at the apex, strongly 3–5 (–7, rarely 9) plinerved, the innermost pair of primary veins diverging from the midrib in an alternate to rarely opposite arrangement 1/5-1/3 of the distance to the apex; primary veins prominent below; margin entire. Inflorescence bearing 3–5 (–8) flowers; peduncle and axis of the inflorescence purple, together 5.5-15 (-19) cm long in flower and 18-24 (-41) cm long in fruit when measured to the furthest pedicel, green or purple, scantily puberulent with hairs 0.1-0.2 mm long; bracts and scales of the inflorescence caducous, translucent white, petaloid,  $7-12 \times 3-9$  mm, elliptic to narrowly obovate, obtuse to rarely emarginate at the apex, concavo-convex, entire; scales 2 or sometimes apparently only one; lower and lateral floral bracts each one per flower. Pedicels 2.0-3.5 mm long. Hypanthium green, 3.0-3.5 mm long, 3.5-4.0 (-5.0) mm wide at the torus. Calyx tube 0.2-0.3 (-0.5) mm long; calyx lobes green or pink to purple, 1.5-2.0 mm long, 2.0-2.5 mm wide at the base, triangular, rounded at the apex. Pedicels, hypanthium, and the margin and both sides of the calyx scantily puberulent, the hairs 0.1-0.2 mm long. Petals white at the base and pink toward the apex,  $11-16(-18) \times 6-10$  mm, oboyate, rounded at the apex, entire. Antesepalous stamens: filaments 4.1-5.0 (-5.5) mm long; thecae yellow, 2.0-2.5 mm long; connective extended 1.6-1.8 mm between the thecae and the insertion of the filament, bearing a dorsal tubercle ca. 0.1 mm long, and a tongue-shaped ventral appendage 0.9-1.3 mm long. Antepetalous stamens: filaments 3-4 mm long; thecae yellow, 2.0-2.2 (-2.5) mm long; connective yellow, extended 0.8-1.0 mm between the thecae and the insertion of the filament, the ventral appendage 0.2–0.4 mm long. The connective in both whorls of stamens bending in late anthesis to bring the thecal pore into contact with the stigma. Ovary ca. 0.3 mm long; style 6.0-6.5 (7.0) mm long, and 1.4–1.6 mm wide where expanded. Fruit 1.0–1.3 mm wide. Seeds ca.  $0.7 \times 0.5 \times 0.4$  mm.

DISTRIBUTION AND PHENOLOGY. — This species of *Monolena* is endemic to Panama where it is found in the provinces of Veraguas and Coclé from the region of the continental divide north to the Caribbean lowlands. It is locally common along rocky streams between 400–1200 meters. Fertile specimens have been collected every month except April, including flowers and fruits in most months.

PARATYPES. — PANAMA. Coclé: El Copé, vicinity of sawmill, north across continental divide, and Alto Calvario, *Antonio 2076* (CAS, PMA), *Croat 44610* (MO), *Croat 68800* (MO), *Galdames et al. 1070* (PMA), *Hamilton & Davidse 2770* (MO), *Hammel 801* (CAS), *Folsom 1595* (MO), *Folsom 3268* (CAS), *Folsom 4118* (CAS, MO), *Folsom & Page 5966* (CAS), *Folsom & Collins 6527* (MO), *Folsom et al. 7089* (CAS), *Read et al. 81-18* (US), *Sytsma 1922* (CAS), *Sytsma & Anderson 4538* (MO), *Warner 420* (MIN); Río Blanco, 2 hour walk down Atlantic slope from sawmill at El Copé, *R. Dressler 5646* (PMA), *Warner 419* (MIN); Río Tife, base of Cerro Tife, *S. Knapp 3708* (MO), *S. Knapp 3719* (CAS, MO); Veraguas: road from Agricultural School Alto de Piedra to Calovébora: Alto de Piedra, *Tam 27* (MO, PMA); Río Primero Brazo, ca. 2.6 km beyond the school, *T. Antonio 2037* (CAS, MO), *Croat 23179* (MO), *Croat 25439* (MO), *Croat 25449* (MO), *Croat & Folsom 34121* (MO), *Mori & Kallunki 4759* (MO), *Warner 418* (MIN); Río Segundo Brazo, *Mass & Dressler 1633* (MO, US); 8.8–11 km from the school, *Mori & Kallunki 3206* (PMA) *Mori & Kallunki 6203* (MO); Río Dos Bocas, *Croat 27406* (MO, PMA) *Croat 27506* (MO), *Mori et al. 3861* (MO); Guabal, between the Continental Divide and Río Calovébora, *Dressler 4719* (MO, PMA, US).

DISCUSSION. — Monolena trichopoda is recognized by the two rows of cilia on the petioles, the leaf blades strongly plinerved with the margins entire, the small number of scales on the inflorescence, and the tongue-shaped ventral appendage on the connective of the antesepalous stamens. On the one hand, these plants share certain features with those of the Cordifolia complex, such as small stature, absence of foliar sclereids, and bending of the connective in late anthesis to bring the thecal pore into contact with the stigma. On the other hand, the blades are lanceolate to elliptic and strongly plinerved, characters not found in the Cordifolia complex. Several specimens from Bocas del Toro, Panama (Santamaria & Lara 952, 964 and 1078, all at PMA) are related to Monolena trichopoda, but are left unassigned pending further study. The petioles on these specimens have a dense pubescence that is perhaps unique for the genus.

ETYMOLOGY. — The specific epithet refers to the ciliate petiole, a character that is unique to this species of *Monolena*.

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